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Short communication

The water use dynamics of canola cultivars grown under elevated CO_2 are linked to their leaf area development

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ABSTRACT

The 'CO_2 fertilisation effect' is often predicted to be greater under drier than wetter conditions, mainly due to hypothesised early season water savings under elevated [CO_2] (e[CO_2]). However, water savings largely depend on the balance between CO_2-induced improvement of leaf-level water use efficiency and CO_2-stimulation of transpiring leaf area. The dynamics of water use during the growing season can therefore vary depending on leaf area development.

Two canola (*Brassica napus* L.) cultivars of contrasting growth and vigour (vigorous hybrid cv. Hyola 50 and non-hybrid cv. Thumper) were grown under ambient [CO_2] (a[CO_2], ~400 µmol mol^{-1}) or e[CO_2] (~700 µmol mol^{-1}) with two water treatments (well-watered and mild drought) in a glasshouse to investigate the interdependence of leaf area development and water use.

Dynamics of water use during the growing season varied depending on [CO_2] and cultivars. Early stimulation of leaf growth under e[CO_2], which also depended on cultivar, overcompensated for the effect of increased leaf-level water use efficiency, so that weekly water use was greater and water depletion from soil greater under e[CO_2] than a[CO_2]. This result shows that the balance between leaf area and water use efficiency stimulation by e[CO_2] can tip towards early depletion of available soil water, so that e[CO_2] does not lead to water savings, and the 'CO_2 fertilisation effect' is not greater under drier conditions.

1. Introduction

Atmospheric CO_2 concentration ([CO_2]) has increased about 30% from ~317 µmol mol^{-1} in 1960 to ~410 µmol mol^{-1} in 2018 (NOAA, 2018). Based on current emission scenarios, [CO_2] is predicted to surpass 700 µmol mol^{-1} by 2100 (IPCC, 2013). Rising [CO_2] drives global climate change including more frequent extreme climate events such as droughts in many cropping areas (IPCC, 2014). As a key substrate for plant photosynthesis, rising [CO_2] also affects plant performance including increases in productivity and yield of C_3 plants through the so-called 'CO_2 fertilisation effect' (Ainsworth and Long, 2005; Gray et al., 2016; Kimball, 2016; Leakey et al., 2009).

The extent of 'CO_2 fertilisation effect' varies with growing conditions and is often assumed to be greater under drier than wetter conditions (Kimball, 2016; Leakey et al., 2009). This assumption is based on the well-documented reduction in stomatal conductance (g_s) and increased leaf-level water use efficiency (Ainsworth and Long, 2005; Bernacchi et al., 2007) by elevated [CO_2] (e[CO_2]). As a result, crop water use during early growth stages is lowered (Kimball, 2016; Leakey et al., 2009) thus conserving more soil water for the critical grain filling period (Burkart et al., 2011; Hussain et al., 2013). This extra soil water potentially extends the grain filling period during which carbon gain can be stimulated by e[CO_2], thus mitigating the effect of drought on crop productivity (Cruz et al., 2016; Wall, 2001).

Recent experimental evidence, however, has reported a diminishing 'CO_2 fertilisation effect' with the intensification of drought (Gray et al., 2016; Jin et al., 2018). The complexity arises because water savings under e[CO_2] are dependent on the balance of gains in leaf-level water

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use efficiency with increases in transpiring leaf area (Morison and Gifford, 1984; Samarakoon and Gifford, 1995). Despite greater leaf-level water use efficiency, greater stimulation of early leaf area under e[CO_2] may increase total transpiration or water use (Ukkola et al., 2016; Wu et al., 2004) and therefore deplete soil water more quickly. Such early depletion of soil water combined with reduced rainfall during grain filling, as predicted in future climate scenarios (Watson et al., 2017), may exacerbate drought effects (Manea and Leishman, 2014). Therefore, the combined effect of e[CO_2] and drought on the seasonal dynamic of leaf growth and water use needs to be addressed simultaneously, especially for crops that have pronounced growth spurts and are sensitive to drought.

Canola (*Brassica napus* L.) is one such crop with distinct growth spurts and high sensitivity to drought (Hess et al., 2015) but is extensively grown in low rainfall cropping areas experiencing regular terminal drought (Maaz et al., 2018). Canola is an important oilseed crop and currently ranks second in global importance as a source of protein for livestock (Högy et al., 2010) and third for vegetable oil (FAOSTAT, 2018). We examined seasonal dynamics of leaf area development and water use under e[CO_2] of two canola cultivars with contrasting vigour and growth rates in glasshouse experiments. This allowed us to test the following hypotheses:

1 Stimulation of leaf growth by e[CO_2] will (over) compensate for greater leaf-level water use efficiency, thus increasing seasonal water use.
2 Considering previous results reporting greater 'CO_2 fertilisation effects' on hybrids (Yang et al., 2009), greater e[CO_2]-induced growth stimulation of a vigorous hybrid cultivar will result in greater water use for that cultivar.

2. Materials and methods

Two canola (*Brassica napus* L.) cultivars with contrasting vigour and growth habit (vigorous hybrid cv. 'Hyola 50′ and non-hybrid cv. 'Thumper') were grown in either an ambient [CO_2] (a[CO_2] ~ 400 μmol mol^{-1}) or an e[CO_2] (~700 μmol mol^{-1}) chamber (glasshouse subdivision) in a glasshouse (Creswick, Victoria, Australia; 37º25′24.2″ S, 143º54′1.6″ E, elevation 465 m). The photoperiod was 14/ 10 h (day/ night), temperatures were 22 ± 2.4/ 13 ± 1.9ºC (mean maximum/ minimum temperature ± SE) and relative humidity 50–60%. The experiment was first run in 2015 and repeated in 2017, with [CO_2] treatments swapped between glasshouse chambers to account for any non-specific chamber effect.

Plants were grown in 'columns' (PVC pipes with 10 cm diameter and 80 cm length; 16 in each CO_2 chamber each year) filled with about 10 kg (dry weight) of soil. The soil was sieved (2 mm) grey sandy loam (sourced from a local field) with pH 6.8, EC 645 μS cm^{-1} and field capacity (FC) of 28% (v/v; determined at equilibrium after three wetting–drying cycles). Nutrients (20 mg N as urea, P as KH_2PO_4 and Mg as $MgSO_4$ as well as 10 mg Zn as $ZnSO_4$, Fe as $FeSO_4$, Cu as $CuSO_4$ and Mn as $MnSO_4$, plus 1.5 g $CaCO_3$ kg^{-1}) were mixed thoroughly throughout the soil.

Ten seeds per column were sown on 5 June and 30 May in 2015 and 2017, respectively and thinned to the most vigorous seedling ten days after sowing (DAS). All columns were maintained close to FC until 40 DAS. Columns were then randomly assigned to one of two treatments, well-watered (WW; maintained at 90% FC) and drought (DD; 50% FC). Soil water treatment was controlled by weighing each column weekly, and replacing water lost through evapotranspiration. Half of the amount of water lost in the previous week was added mid-week to avoid excessive fluctuations of soil water. Volumetric soil water content (SWC) was measured weekly (before water adjustment) at four depths (10, 30, 50 and 70 cm) in the soil columns using a time domain refractometer (TDR, Theta probe ML3, Delta-T Devices Ltd., Burwell, Cambridge, UK; with factory default calibration) inserted horizontally into the soil.

Stomatal conductance (g_s) and net photosynthetic assimilation rate (A_{net}) were measured on one randomly selected, fully expanded young leaf at mid-plant height in each column. Measurements were taken weekly from 78 to 120 DAS with an infrared gas analyser with a standard leaf chamber (clear-top 2 × 3 cm, Li-6400, Li-Cor, Lincoln, NE, USA). Flow rate was set to 500 μmol s^{-1} with either 400 or 700 μmol mol^{-1} of [CO_2] for plants grown in a[CO_2] and e[CO_2] chambers, respectively. Measurements were made on sunny days between 0930 to 1130 h with photosynthetically active photon flux density at the leaf level of 600 to 850 μmol m^{-2} s^{-1}. Vapour pressure deficit (VPD) and leaf temperatures varied between measurement days but not between treatments within the same date (VPD ranged from 0.8 and 2.7 kPa). Readings were taken after first stabilisation (after about 1.5 min) to capture data close to growing conditions. Chlorophyll content was measured weekly on six leaves with a SPAD meter (SPAD-502, Konica Minolta, sensing, Inc. Japan) in each column.

Sampling took place at an approximately fortnightly intervals and leaf area was measured using a leaf area meter (LI-3100C Area Meter, Licor, Lincoln, NE, USA). Dropped leaves from individual plants were collected periodically, oven dried (at 70 °C for 72 h) and weighed to determine senescent leaves. The parameter 'cumulative senescent leaves' was calculated as the sum of dropped leaf weight over time.

2.1. Statistical analysis

The experimental design was a nested, randomised split-plot design with two [CO_2] (main-plots, i.e. glasshouse chambers). The two cultivars and two water treatments were nested within the CO_2 treatment with 4 replications for a total of 2 × 2 × 2 × 4 = 32 experimental columns in each of the two years. The effect of DAS, CO_2, cultivars, and water treatments were considered fixed effects and year and column ID as random effects (for data collected only in 2017 such as A_{net}, g_s, soil water content and SPAD value only column ID used as random effect) and were evaluated using linear mixed effects models with R package 'nlme' (Pinheiro et al., 2018). Homogeneity of variances was evaluated visually, and the model was adjusted when stepwise evaluation of the model showed an improvement. Data analysis was performed in R version 3.4.3 (R Core Team, 2017) and mixed effects model P-values are reported in supplementary Table S1.

3. Results

3.1. Leaf gas exchange

Elevated [CO_2] stimulated A_{net} of canola with this effect greater under WW than DD conditions (Fig. 1A, supplementary Table S1). The cv. Thumper had greater A_{net} than cv. Hyola 50. Stomatal conductance was lower under e[CO_2] than a[CO_2] but their differences diminished as the growing season progressed (Fig. 1B). Elevated [CO_2] induced reduction of g_s was greater under WW than DD. As the growing season progressed, g_s decreased subsequently and this reduction was greater under WW than DD. The cv. Thumper had greater g_s than cv. Hyola 50.

3.2. Leaf area and leaf senescence rate

Elevated [CO_2] stimulated leaf area. This stimulation was highest during the period of maximum vegetative growth and diminished later in the season (Fig. 2). Elevated [CO_2]-stimulation of leaf area was greater for cv. Thumper than cv. Hyola, and greater under WW than DD conditions. Although the vigorous hybrid cultivar (Hyola 50) showed slightly greater e[CO_2]-stimulation of leaf area during early growth stages, once maximum vegetative growth was reached, e[CO_2]-stimulation of leaf area was greater for the non-hybrid cultivar (Thumper) than Hyola 50. Senescence (shedding) of leaves began and peaked earlier under e[CO_2] than a[CO_2] (Fig. 3A). Leaf senescence was faster

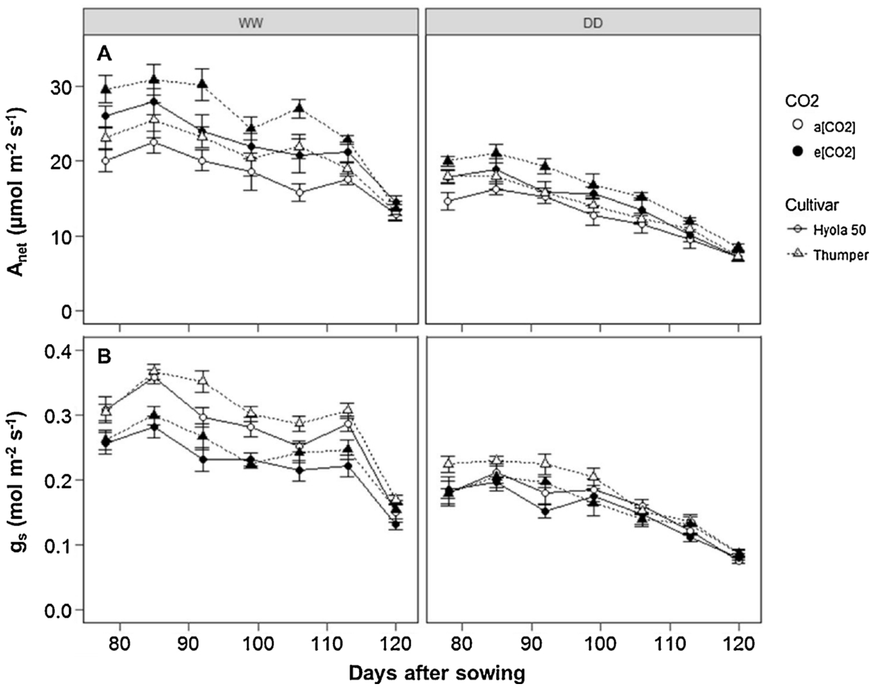

Fig. 1. (A) Net photosynthetic assimilation rate (A_{net}) and (B) stomatal conductance (g_s) of canola (*Brassica napus* L.) cv. Hyola 50 and cv. Thumper grown under ambient [CO_2] (a[CO_2], ~400 μmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~700 μmol mol^{-1}) with contrasting water treatments (started 40 days after sowing), well-watered (WW) and drought (DD) in 2017. Mean and SE of n = 4 replicates per treatment and cultivar combination.

under WW than DD. Differences in cumulative senescent leaves between a[CO_2] and e[CO_2] increased from the start of leaf shedding but diminished later in the season (Fig. 3B). SPAD values decreased earlier under e[CO_2] than a[CO_2] (supplementary Fig. S1).

3.3. Weekly and cumulative water use

During the early growth stages, weekly water use was greater under e[CO_2] than a[CO_2] but as the season progressed this trend reversed (Fig. 4A). Similarly, cv. Hyola 50 had greater weekly water use than cv. Thumper during the early growth stages, but later in the season the difference was reversed. Despite greater weekly water use during the early growth stages, the difference in cumulative water use between a[CO_2] and e[CO_2] over the whole growing season was diminished when provided with WW conditions (Fig. 4B). In contrast, under DD cumulative water use was greater under e[CO_2] than a[CO_2]. Supporting the weekly water use data, SWC was lower under e[CO_2] than a[CO_2] during the early growth stages, but there were no detectable differences later in the season (Fig. 4C). During the early growth stages, SWC of cv. Hyola 50 was lower than cv. Thumper, but this trend was reversed later in the season.

4. Discussion

One major driver of soil water depletion is canopy transpiration (Nelson et al., 2004), which is a function of both g_s and leaf area (Samarakoon and Gifford, 1995). The drought treatment in our current study caused detectable reductions in g_s, but g_s remained above 100 mmol m^{-2} s^{-1}, for most of the experiment, indicating only mild stress that may limit photosynthesis through restricted CO_2-diffusion, but is unlikely to cause any physiological damages (Flexas et al., 2006). In the current study, greater A_{net} (Fig. 1A) under e[CO_2] markedly increased plant growth and consequently transpiring leaf area (Fig. 2), which corresponds to earlier findings for canola (Faralli et al., 2017; Qaderi and Reid, 2005), grasses (Manea and Leishman, 2014) and other crops (Ainsworth and Long, 2005; Bunce, 2016) from [CO_2] enrichment studies.

Whilst many studies reported a greater 'CO_2 fertilisation effect' under drought, these were usually obtained from environments that experienced naturally high rainfall or were continuously irrigated (Kimball, 2016; Leakey et al., 2009). In such environments, greater 'CO_2 fertilisation effect' under drought might be attributed from delaying the onset of water stress due to lower water under e[CO_2] (Cruz et al., 2016, 2018). In contrast, our results show the high temporal variability of the responses of crop water use to [CO_2]. This variability has also been reported under field conditions, where severe drought precluded any benefits from e[CO_2] (Gray et al., 2016; Jin et al., 2018). In our present experiment, stimulation of leaf area under e[CO_2] lead however to greater water use, not water savings, during the early growth stages irrespective of water treatments and cultivars (Fig. 4A).

The difference in leaf area between plants grown in different [CO_2] decreased, and even reversed later in the season, because e[CO_2]

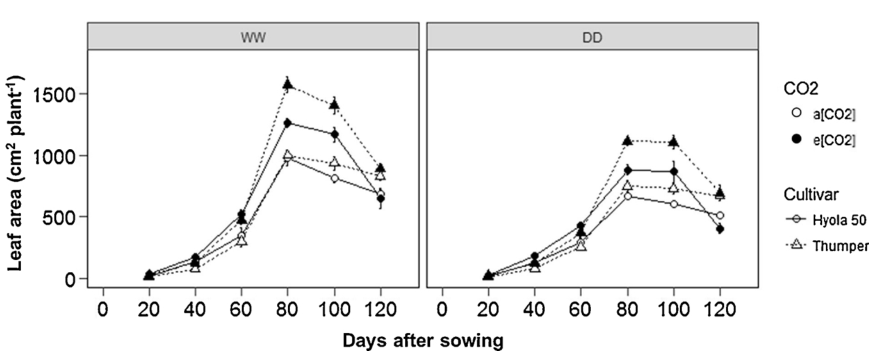

Fig. 2. Leaf area of canola (*Brassica napus* L.) cv. Hyola 50 and cv. Thumper grown under ambient [CO_2] (a[CO_2], ~400 μmol mol^{-1}) or elevated [CO_2] (e[CO_2], ~700 μmol mol^{-1}) with contrasting water treatments (started 40 days after sowing), well-watered (WW) and drought (DD) in 2015 and 2017. Mean and SE of n = 8 replicates per treatment and cultivar combination.

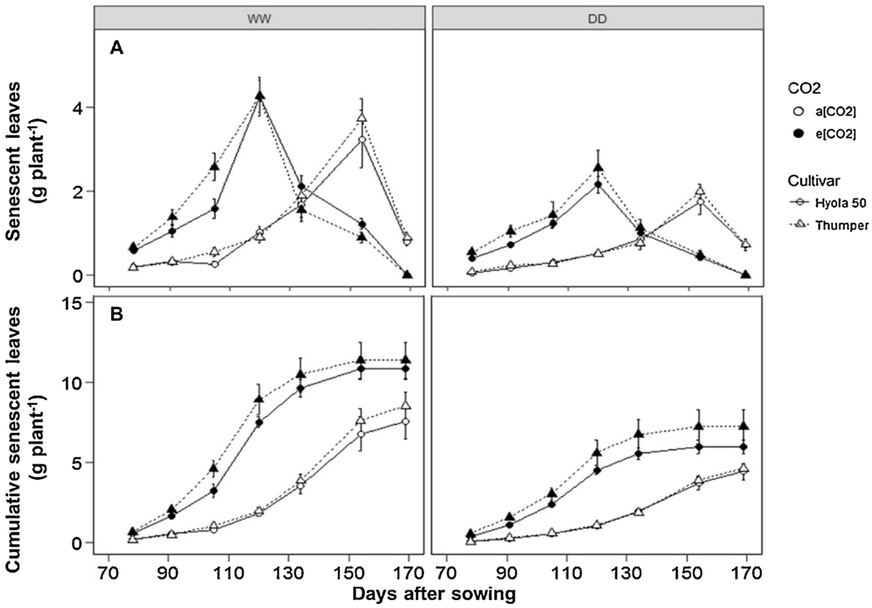

Fig. 3. Senescent leaves (A) and cumulative senescent leaves (B) of canola (*Brassica napus* L.) cv. Hyola 50 and cv. Thumper grown under ambient $[CO_2]$ ($a[CO_2]$, ~400 μmol mol^{-1}) or elevated $[CO_2]$ ($e[CO_2]$, ~700 μmol mol^{-1}) with contrasting water treatments (started 40 days after sowing), well-watered (WW) and drought (DD) in 2015 and 2017. Mean and SE of n = 8 replicates per treatment and cultivar combination.

caused faster leaf shedding (Fig. 3A; B and S1). Early onset of chlorophyll degradation and leaf shedding was previously reported for canola under $e[CO_2]$ (Franzaring et al., 2011). Due to strong coupling between leaf area and water use (Morison and Gifford, 1984; Samarakoon and Gifford, 1995), weekly water use later in the season was greater under $a[CO_2]$ than $e[CO_2]$. As leaf chlorophyll content is a key indicator of the plant photosynthetic capacity (Cannella et al., 2016), greater chlorophyll content may indicate the maintenance of plant physiological processes for longer under $a[CO_2]$, corresponding to greater water use late in the season (Fig. 4A).

Following the trends of leaf area and weekly water use cumulative water use was greater under $e[CO_2]$ than $a[CO_2]$ early in the season however, this trend was inconsistent across water treatments later in the season. Faster leaf shedding in conjunction with $e[CO_2]$-induced greater reduction of g_s under well-watered conditions reversed the weekly water use and resulted in no apparent change in cumulative water use between $a[CO_2]$ and $e[CO_2]$, which is in line with some earlier studies (Hunsaker et al., 2000; Kimball et al., 1999). In contrast, under drought conditions, $e[CO_2]$-induced lower reduction of g_s in conjunction with greater leaf area delayed the reversal of water use differences between $a[CO_2]$ and $e[CO_2]$. This extended period of greater water use translated into greater cumulative water use under e

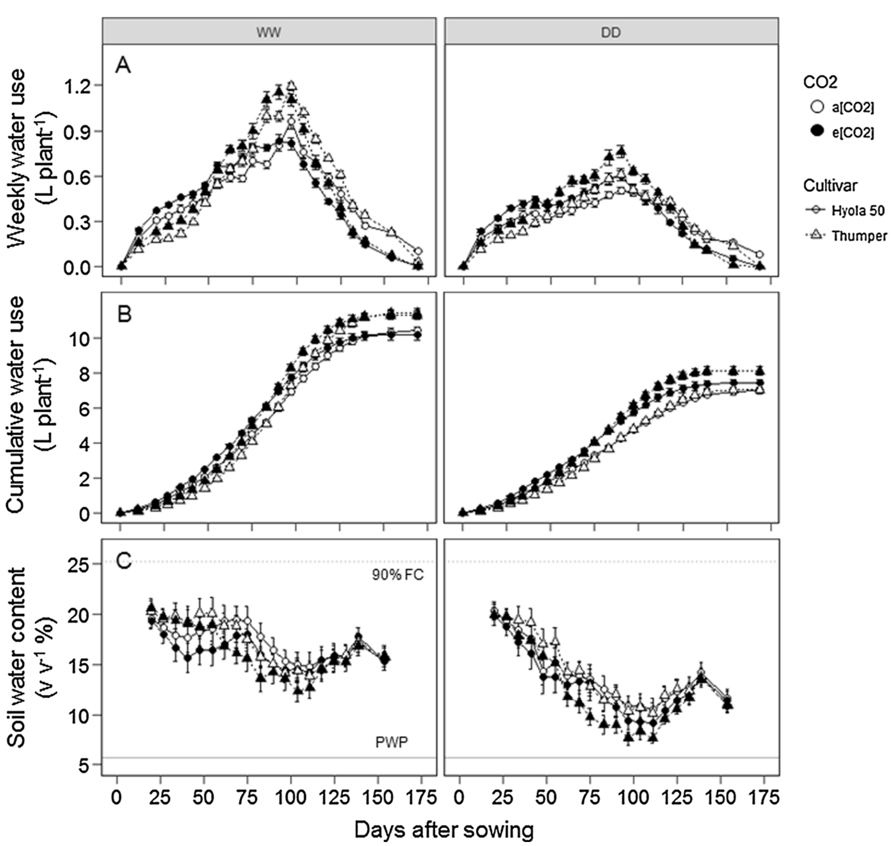

Fig. 4. Weekly (A) and cumulative (B) water use and (C) soil water content (SWC) of canola (*Brassica napus* L.) cv. Hyola 50 and cv. Thumper grown under ambient $[CO_2]$ ($a[CO_2]$, ~400 μmol mol^{-1}) or elevated $[CO_2]$ ($e[CO_2]$, ~700 μmol mol^{-1}) with contrasting water treatments (started 40 days after sowing), well-watered (WW) and drought (DD) in 2015 and 2017 (SWC in 2017 only). Mean and SE of n = 8 (n = 4 for SWC and each replicate is an average of 4 values measured at 10, 30, 50 and 70 cm depths of the soil column) replicates per treatment and cultivar combination. Soil water content at 90% of field capacity (FC; dotted grey line) and at permanent wilting point (PWP; adapted from Veihmeyer (1956); solid grey line) are indicated by horizontal lines.

$[CO_2]$ compared to $a[CO_2]$ over the life of the crop (Wu et al., 2004).

'Vigorous' hybrid cultivars of rice were reported to respond proportionally more to $e[CO_2]$ than conventional cultivars, due to stronger sink generation and an enhanced capacity to utilize the carbon sources in a high $[CO_2]$ environment (Liu et al., 2008; Yang et al., 2009). In only partial support of this hypothesis, $e[CO_2]$-stimulation of leaf area seemed greater for the hybrid cultivar, but only during the early growth stages. Later on, the $e[CO_2]$-stimulation of leaf area was greater for the non-hybrid cultivar. Greater A_{net} coupled with the $e[CO_2]$-stimulation of greater leaf area during the grain filling period resulted in greater 'CO_2 fertilisation effect' for non-hybrid canola cultivar than hybrid (Uddin et al., 2018). Compared to hybrids, some non-hybrid cultivars showed similar responses to $e[CO_2]$ for rice (Zhu et al., 2015) and some even greater responses for wheat (Benlloch-Gonzalez et al., 2014); although such comparisons may depend on growing conditions and timing of the measurements. Weekly water use, and, correspondingly, SWC of two cultivars studied was strongly related to their leaf area development, which followed similar patterns throughout the growing season.

Our study demonstrates that early stimulation of leaf growth under $e[CO_2]$ can overcompensate for the effect of increased leaf-level water use efficiency on water use in the short term, resulting in canola depleting more soil water under $e[CO_2]$ than under $a[CO_2]$, even under mild drought conditions applied in the glasshouse. In line with recent experimentation where drought stress was more pronounced (Gray et al., 2016; Jin et al., 2018), our finding contradicts the widely cited mechanism of greater 'CO_2 fertilisation effect' under drier than wetter conditions (Kimball, 2016; Leakey et al., 2009), and demonstrate that the dynamically changing balance between $e[CO_2]$-effects on leaf area and water use efficiency can lead to such apparently contradicting results. In water-limited Mediterranean regions, which are most often vulnerable to severe and terminal drought, this greater leaf area and increased water use under $e[CO_2]$ coupled with the predicted reduction in growing season rainfall and rising global temperature, may increase the risk of haying-off (Nuttall et al., 2012; van Herwaarden et al., 1998). The effect of $[CO_2]$ on water use throughout the growing season was linked with the response of leaf area to $[CO_2]$. Following the seasonal trend of leaf area, both cultivars showed temporal asynchrony in water use and soil water depletion patterns; furthermore, there were CO_2 and WT effects.

Authors contributions

Shihab Uddin: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Shahnaj Parvin: Data curation; Investigation; Methodology; Validation; Writing - review & editing.

Markus Löw: Conceptualization; Formal analysis; Methodology; Resources; Supervision; Validation; Writing - review & editing.

Glenn J Fitzgerald: Funding acquisition; Project administration; Resources; Supervision; Writing - review & editing.

Sabine Tausz-Posch: Funding acquisition; Project administration; Resources; Writing - review & editing.

Roger Armstrong: Funding acquisition; Project administration; Resources; Writing - review & editing.

Michael Tausz: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jplph.2018.08.001.

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